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THE GEOGRAPHIC DISTRIBUTION OF CLOSELY RELATED SPECIES.¹

BY ROBERT GREENLEAF LEAVITT.

THE botanical researches of the members of the New England Botanical Club are largely taxonomic and floristic. With some of us this is vocation, with others avocation. The majority perhaps pursue the study of plants in the field and make collections of them in herbaria for their own personal satisfaction. Floristic studies may properly be an end in themselves, whether followed as a business or only for recreation. In the latter case they need no further justification than the fine and pure pleasure they afford to those who love them for themselves. But the results of these studies, for whatever conscious motive pursued, may have an application and a destination far beyond our private aims. Collections of specimens and reports of distribution recorded in accessible journals by well-informed non-professional as well as professional botanists, may help materially in answering some of the largest questions of biological science. In this paper I hope to make it clear that refined taxonomy and most thorough-going plant geography may have a direct relation to the enormously difficult problem of evolution.

Organic geography has, indeed, already served the cause of evolution,—in aiding to secure general acceptance of the Descent Theory. Darwin and Wallace, drawing upon the works of taxonomers, were able to point to features in the distribution of

¹ A paper read before the New England Botanical Club at the meeting of Feb. 1, 1907. Published as Contribution from the Ames Botanical Laboratory, no. 6.

species which support the notion of common descent. Plants and animals, they said, occur upon the surface of the globe just as if they had originated by evolution, and in a manner unintelligible on the assumption of special creation. Species are universally found in the neighborhood of other species which they resemble; or to put this generalization in evolutionary phrase, species arise in geographic proximity to the species from which they may be supposed to have sprung. The geographic evidence was an important part of the testimony accumulated by Darwin ('59), to which he gives two of the fifteen chapters of the "Origin of Species." Wallace ('55) had already published an essay arguing for the evolutionary conception of organic history, the main thesis being this: "Every species has come into existence coincident both in time and space with a pre-existing closely allied species." Thus the evolutionist has been under deep obligation to the taxonomer from the beginning.

The obligation is likely to be much increased with the lapse of time. I do not agree with D. H. Scott, that the determination of the actual course of descent is the ultimate, or chief, object of the scientific systematist.¹ The fact of evolution being admitted, and the course of evolution having been ascertained, there still remains the question, "By what methods have new forms emerged from old ones?" — a subject not less interesting or important than the others, from any point of view. It seems to me, furthermore, that the final goal of phytogeography is not reached in the reconstruction of the continents and islands of former epochs, and the reviving of ancient states and changes of climate, through the study of the history of the vegetation of the earth; nor is its purpose satisfied in teaching us through its ecological aspects, that plants are marvellously and multifariously adapted to their environments. Biologically considered, there is a still more valuable product yet to be yielded by these sciences. Organic geography will, I believe, unite with systematic botany and zoölogy and with experimental morphology in composing the solid basis of an adequate theory of evolution.

¹ The present Position of Palæozoic Botany, Lotsy's *Progressus Rei Botanicae*, 1: 139 (1907).

The finely discriminative work of modern taxonomers, much as it confuses and discourages students of other aspects of biologic science, is necessary for several reasons but especially is it necessary from the point of view of the evolution problem. Doubtless systematic and experimental work will be more frequently coöperative henceforth, and such studies as those of Alexis Jordan, de Bary, Rosen and Wittrock will be repeated with many of the so-called polymorphic plant groups by students of the greater problem.

This view is apparently opposed to that lately expressed by a prominent worker in experimental evolution, who seems to deny this applicability. "The underlying fault," he says, "consists in the fact that taxonomic and geographic methods are not in themselves, or conjointly, adequate for the analysis, or solution, of genetic problems. The inventor did not reach the solution of the problem of the construction of a typesetting machine by studying the structure of the printed page, but by actual experimentation with mechanisms, using printed pages only as a record of his success. Likewise no amount of consideration of fossils, herbarium specimens, dried skins, skulls, or fish in alcohol may give any actual proof as to the mechanism and action of heredity in transmitting qualities and characters from generation to generation, although from such historical data the general trend or direction of succession may be traced." — MacDougal (:06, p. 4).

Nevertheless, it may be shown that, while such studies are not in themselves adequate to the solution of genetic problems they have a very high corrective and evaluatory worth.

Geographic studies founded on an exact taxonomy have a corrective function. It is axiomatic that no theory having its origin in experiment can be accepted if it seems to be in fundamental discord with what we know of the present disposition of the organic world. For example, the theory of Mutation as developed by de Vries cannot be accepted for the animal kingdom, if, as seems to certain zoölogists, it is irreconcilable with the facts of the distribution of animals. And even if an hypothesis is not positively excluded by the facts, it may be weakened or practically nullified by comparison with large bodies of facts

gathered broadly; so that we may fairly ask the experimental school to admit that results, however well proved for the conditions established by the experimenter, ought to be assigned little worth if they find only a trivial correspondence in nature at large. We make the same demand of the physiologist with respect to such a phenomenon as geotropism, for instance. The extended study of this form of irritability has its justification only in the fact that plants in nature so widely show the effects of geotropism in their forms; the value of the experimental results is great because the phenomenon is manifestly widespread in free nature, being observable in the erect attitude of countless main axes in field and forest, in the fixed angles of side stems, the vertical descent of tap-roots, etc., etc. In like manner a true theory of specific origins should find strong confirmation in the study of the broadest aspects of plant and animal life. Every grand agent of specific modification should leave its distinctive mark upon the character of life as a whole, and if we rightly apprehend the nature of the agent we may expect to be able to distinguish its special mark or effect when we know plants and animals thoroughly. I think that it will appear from considerations which I now bring before you that the distribution of species must have peculiarities corresponding to the particular class of evolutionary forces which have been at work. If this be so, suitable studies in geographic taxonomy must possess high evaluatory worth when we wish to estimate theories of evolution.

THE EFFECTS OF DIFFERENT EVOLUTIONARY AGENCIES UPON SPECIFIC DISTRIBUTION

Let us examine the necessary effects of the chief supposed evolutionary agencies upon the character of specific distribution; and first contrast Natural Selection in Darwin's stricter sense with Mutation, in this regard. Natural Selection works within specific limits. Its materials are the small, or individual, variations within the species. By the accumulation of these variations as they occur from generation to generation new characters are built up. The change in a species is slow and the whole species within a given competitive area moves along together. When

we consider that sufficient change has occurred to warrant the epithet 'new,' as applied to the condition of the group, we find that the new species has risen upon stepping stones of its dead self, since the survival of the fittest has had its converse in the extinction of the unfit — that is, the 'old' species —; and in the given area only a single new species is found replacing the vanished old one. For any given area of competition the transforming effect of Natural Selection then, is monotypic. Romanes (:06, ch. I.) clearly states the truth that Natural Selection without isolation effects monotypic evolution, and only by the aid of isolating factors of some kind results in polytypic evolution. Nägeli's earlier exposition of the monotypic effect of Natural Selection was explicit (Nägeli, '73).

On the other hand Mutation breaks the species and momentarily at least, must give a polytypic aspect to the group within a specific area. The parent species is contemporaneous with the new species to which it gives rise. The new and the old stand side by side for a time, without geographic isolation and in general without isolation of any sort. This is the primary condition. Subsequently competition may leave only one of the several original forms in an area. In some instances topographic (ecological) separation of the mutants, or chroral isolation in respect to flowering or breeding time, a physiological isolation may be the immediate result of Mutation. But as a rule the first effect of Mutation must certainly be the allocation of closely related species, or kinds, in the same area without any sorting or separation.

If we compare Orthogenesis, acting under guidance of the environment, with Natural Selection on the one hand and Mutation on the other, we see that Orthogenesis must in many respects agree with Natural Selection rather than with Mutation as concerns the distribution of its products — species. Throughout a single region of uniform ecological character the effect of environmental moulding, so-called, upon a given organic stock must be monotypic. But if the ecological conditions are diverse in a geographic district, as they always are when the surface is varied, we may expect to find as many kinds of plants or animals derived from a single stock as there are ecologically different environ-

ments in the district; or, if interbreeding suffices to reduce the diversity in some degree, at least several kinds perfering different habitats. While in the broader geographic sense this effect would be polytypic, in that any geographic district might have several different closely allied types, each type would fit a particular set of conditions; there would be definite allotment and topographical separation of the derivative species, and each ecological field would present a monotypic aspect. A distribution quite distinct from that due to recent Mutation would be found.

Thus while the geography of species may or may not be decisive as between the evolutionary theories known by the names Natural Selection and Orthogenesis, both these modes are distinguished from Mutation in the immediate effects which they have upon distribution. Such specific distribution as Moritz Wagner asserted to be universal or almost universal, if it could be proved, would be practically fatal to the Mutation Theory regarded as a general explanation of specific evolution.¹

It is hard to see on what ground the experimentalists can deny the competence of geographic evidence. Indeed they appear at times to recognize the propriety of the appeal to nature; De Vries refers to *Draba*, *Viola* and similar groups, and MacDougal in the paper already cited alludes to studies of plant distribution and adduces the case of closely related *Opuntias* in the Arizona desert. The distinguished zoölogist who recently assumed to pass upon the merits of the Mutation Theory, evidently without

¹ Yet Darwin (Orig. Sp., ch. IV.) in his theory of Divergence of Character, seems to allow polytypic evolution within an area by means of Natural Selection. He thinks geographic isolation unnecessary. Weismann (:04, 2: 338) argues against the necessity of isolation and for a polytypic condition as possibly arising by Natural Selection, alleging in support of this view sexual dimorphism, and polymorphism in species of animals. To which it may be replied that we do not know whether the diverse forms in the same species of animals have arisen by Natural Selection. In the absence of evidence, the contention becomes a theoretical one, in which Romanes ('86, pp. 343, 386), Gulick ('88, pp. 202-206) and Nägeli seem to have the clearer views, and I have accepted their opinion. Whichever side is taken, *it has to be allowed that a uniformly monotypic geographic distribution excludes Mutation.*

much knowledge of De Vries's work and apparently after a reading of only the popular lectures published in this country,¹ was at least thus far right, that he searched for indications of mutation in the distribution of animals. The evidences should be found even in museums, providing the museums are representative, and providing mutation is a sufficient explanation of the origin of species.

THE NECESSITY OF ISOLATION: MENDELIAN INHERITANCE

Before coming to an examination of the facts as they are represented by writers, it will be well to consider for a moment a theoretical side of the subject, namely the supposed *necessity of isolation* as a factor in the evolutionary process. Granting that new forms may appear upon the scene by Mutation, what is to become of them? How can Mutation be said to originate new species — that is, stable groups — if through interbreeding the mutants are at once swallowed up by the parent species with which they grow commingled? The opponents of the Mutation Theory hold that the isolation which the experimenter practices in his garden by means of paper bags, etc., is lacking in nature and that this difference between the garden and free nature vitiates the experiments.

The need of isolation is well, and for the present sufficiently, discussed in the writings of Romanes and Gulick; the latter has treated every form of isolation in an exhaustive fashion, chiefly from the theoretical standpoint and upon the basis of the very limited knowledge of heredity of a few years ago. The conclusion of these authors is that some kind of segregation or isolation is necessary for the success of a new race. While Wagner ('89) saw only spatial isolation as giving the needful security, Romanes (:06) and Gulick (:05) have shown, as well as can be shown deductively, that other forms of isolation may suffice, such as

¹ Is it too much to ask that those who undertake to discuss deVries's theories shall read his evidence? The lectures in English (*Species and Varieties*, Chicago, 1905), doubtless serve a useful purpose in popularizing, but incidentally have done some harm in leading certain critics to suppose that they may find therein an adequate exposition of principles and evidence.

difference of breeding time, difference of local habitat, and physiological properties precluding inter-breeding. The clear discussions of Romanes and Gulick have rendered superfluous much in recent disputes on Isolation and Evolution.

Lately new conceptions in the theory of heredity have materially changed the conditions of the argument. Experiment has shown that new characters may not be immediately swamped by promiscuous breeding, but may on the contrary, in the fusion of new and old races, predominate in full force over old characters which they sometimes have the power of entirely subduing.¹ While this result is very suggestive, too little is as yet positively known to make an extended discussion at all profitable. Those who are inclined to argue the matter may well take caution from Davenport's opinion on the integrity of unit characters. "While admitting, thus, the reality of unit characters, the further study of the evidence of hybridization in poultry has led me away from the conception that they are rigid and immutable as atoms are, which may be combined and recombined in various ways and always come out of the process in their pristine purity. This is by no means the case. Very frequently, if not always, the character that has been once crossed has been affected by its opposite with which it was mated and whose place it has taken in the hybrid. It may be extracted therefrom to use in a new combination, but it will be found to be altered. This we have seen to be true for almost every characteristic sufficiently studied — for the comb form, the nostril form, cerebral hernia, crest, muff, tail length, vulture hock, foot feathering, foot color, ear lobe, and both general and special plumage color. Everywhere unit characters are changed by hybridizing.

"How does this fact bear on the rival theories of evolution? It has an important bearing on them. It is not in accord with the statements of de Vries quoted above: 'The characteristics of organisms are built up of units that are sharply separable one from another,' and 'Transitions exist between the units as little as between the molecules.' Single comb is one unit and pea

¹ Besides the Mendelian results see also de Vries (: 03, 2, p. 396 *et seq.*) on the crossing of mutants with the parent species.

comb is a different unit, but they are not sharply separable. Crest and no crest are units, but they run into each other in hybridizing. Unit characters may show transitions, and, if so, they may have originated gradually, so far as I see. It does not follow that they must have originated gradually" — Davenport (:06, p. 80).

Castle and Forbes's results with guinea pigs indicate the same modifiability of unit characters. These authors (:06, p. 13) say: "From the foregoing observations it is clear that, while the long-haired and short-haired conditions are sharply alternative to each other in heredity, the gametes formed by cross-breds are not in all cases pure. Frequently they consist of a blend or a mixture of the two alternative conditions, constituting in effect a new condition intermediate between the other two. A study of other characters alternative in heredity yields results somewhat similar.

"Albinism is, in heredity, the most sharply alternative of characters, yet cross-breeding between albino and pigmented guinea-pigs may modify the character both of the albino race and of the pigmented one. This modification may take on a variety of forms, as has elsewhere been pointed out (Castle, :05). It may result in the production of mosaics (pigmented animals spotted with white), or of albinos with a modified peripheral pigmentation, or of albinos visibly like their ancestors but transmitting a different set of latent characters. Again, the rough or rosetted coat of certain races of guinea-pigs is sharply alternative to smooth coat, yet cross-breeding of rough with smooth races may induce curious modifications of the rough character or produce smooth individuals bearing the merest trace of the rough character.

"All these facts are in harmony with the hypothesis, for which there is strong evidence on the cytological side, that each separately heritable character is represented by a different structural element in the germ (egg or spermatozoon). In fertilization the paternal and maternal representatives of a character become more or less closely united, this union persisting through all subsequent cell-generations until the new individual forms its sexual elements. At that time the paternal and maternal representatives of a character separate from each other and pass into different cells.

"But the paternal and maternal representatives of a character may in the meantime have exercised on each other a considerable influence. In the case of some characters, as ear-length in rabbits (Castle, :05a), they completely blend and intermingle, so that a new character is produced strictly intermediate between the conditions found in the respective parents.

"In other cases the modification may be slight, as if the paternal and maternal representatives of a character had been scarcely more than approximated. Sometimes in cases of alternative inheritance no influence of the cross is observable in certain of the 'extracted' individuals, but if any considerable number of individuals is examined, others will be found in which the cross-breeding manifests its influence. From this we conclude that gametic purity is not absolute, even in sharply alternative inheritance."

These are very interesting qualifications of the Mendelian principle of gametic purity. They suggest that new characters might be swamped by repeated crossing, unless they were of such overwhelming importance that they quickly won out in the struggle for existence, to the immediate extinction of the bearers of the older alternative characters. However, discussion may here well wait upon further discovery.

But this may be said: If characters are gradually modifiable, time becomes a necessary element in experiments on evolution and possibly long periods of time may be needed for the demonstration of certain slow natural processes. For the present we may well hesitate to accept the conclusion that Mutation is the sole and only possible mode of evolution. Refreshing as the new method of research is, in the midst of oceans of tiresome speculations, and most valuable and even absolutely indispensable as the results already are, the latter are certainly small compared to the bulk of our ignorance regarding morphogenetic processes. Those who are free from inexpugnable prejudice on the one hand and from infatuation with new ideas on the other, will look for some independent means of estimating the probable significance of the new theories. It is the chief object of this paper to suggest that such estimation may be rested upon the evidence of organic geography when the evidence is available in sufficient body.

If we were right in what was said above about the specific effects of different modes of evolution upon distribution, the first question to be asked of the geographer is this: Are species universally so distributed that each one occupies a region of its own, or a habitat of its own; so that even the nearest related species are strictly separated in space, either in the broad geographic sense, or at least topographically?

It is to be noted that the inquiry has two steps, or stages. The first relates to the distribution of organisms in the broader sense, and it is inquired whether closely related species are found in identical districts, or have largely coincident ranges, in many cases. The adherents of the Mutation Theory expect to find a considerable proportion of such instances. Certain of its opponents have believed that the advance of the theory might be blocked on this first level. But if their efforts fail here they are prepared to fall back upon the second line of defence. The second stage of the inquiry relates to topographical distribution, or distribution in relation to ecological conditions, and asks whether any of the allocated forms — if some are found — exist side by side without even local segregation. Disciples of de Vries expect that instances will occur in such numbers as to satisfy the demands of their theory; while the opposite party thinks that practically no instances will be discovered giving countenance to the idea of Mutation. They expect that all cases of general geographic coincidence of range will be accounted for by ecological segregation, affording practical isolation; and so hope to withstand the final assault of the Mutationists.

The application of the botanical evidence presented in this paper is to the first stage of the inquiry. Some of it is manifestly applicable to the second stage also.

SPECIFIC DISTRIBUTION IN THE ANIMAL KINGDOM

We may briefly review some of the chief contributions to our knowledge of the distribution of animal species. Moritz Wagner, Professor of Zoölogy in Munich, perceived the close relation which distribution may have to the problem of evolution and began to publish upon this subject very shortly after the appear-

ance of Darwin's *Origin of Species*, first as an advocate of the theory of Natural Selection, but shortly as its opponent. Through twenty years of controversy he insisted upon the inadequacy of Natural Selection, and as the prime factor in the diversification of species sought to substitute Spatial Separation and to establish his own Law of Migration and Colony-formation. He supposed a new species to arise by the migration or escape of a single individual or of a pair from the domain of the old species into new territory, where in geographic isolation and freedom from the influence of the old stock a new race might be founded. The divergence of the race from the old type he supposed to result (Wagner, '89, pp. 286-295, 401) (1) from the individual peculiarities of the parental pair or individual, which peculiarities in the absence of the normalizing influence of interbreeding with the whole body of the old stock would necessarily become accentuated; and, (2) from the new environment. His theoretical views, which throughout are questionable, are of less consequence than the facts which he adduced in their support; the facts indeed upon which he first formed these views. Wagner himself was a traveler, observer, and collector in several parts of the world and continually recurs in his writing to his experience in the field with regard to endemic, narrowly restricted species-forms and constant local varieties occurring in overwhelming numbers. His illustrations are drawn from all classes of animals and to some extent also from plants. He represents specific distribution as having a strictly mosaic or chain-like character. Everywhere we find vicarious species and local races in separate habitats. The facts are presented at great length and with careful detail, and seem to form a consistent body of knowledge, which impresses one as being pregnant with a rational principle of wide import.

Mr. C. H. Merriam about a year ago addressed the zoological section of the American Association for the Advancement of Science on the topic, "Is Mutation a factor in the evolution of the higher vertebrates?"—(Merriam, :06). While many of the arguments and conclusions regarding evolutionary processes belong, to my mind, too largely in the conjectural category, and while this author's grasp upon the real character of de Vries's work and upon his theory seems comparatively feeble, the data

of distribution brought forward for several groups of mammals are valuable. Dr. Merriam considers the geographic relations of certain American rats, chipmunks, and ground squirrels; and refers besides to other groups. His representation of specific distribution agrees with that held by Wagner, with a qualification. Merriam shows that the mammals in question occupy distinct areas with very little exception, but that the areas often overlap, and that the overlaps are likely to constitute narrow transition zones characterized by the presence of intergrades. Actual physical barriers are often wanting.

President David Starr Jordan has also discussed the Mutation question from the standpoint of organic geography and assembled from his own experience and that of others a considerable body of evidence regarding birds, while he himself speaks for fishes (Jordan, :05). His paper, which appeared in *Science* a little more than a year ago, contains some extraordinarily sweeping assertions. He says: "...Moritz Wagner (1868) first made it clear that geographical isolation (räumliche Sonderung) was a factor or condition in the formation of every species, race, or tribe of animal or plant we know on the face of the earth." The principles set forth by Wagner "have never been confuted,¹ scarcely even attacked, so far as the present writer remembers, but in the literature of the present day they have been almost universally ignored." The question is much discussed whether minute variations may serve to establish a new species in the presence of a parent species, or whether wide fluctuation or mutation may do so. "In theory either of these conditions might exist. In fact both of them are virtually unknown. In nature a closely related distinct species is not often found quite side by side with the old. It is simply next to it, geographically or geologically speaking, and the degree of distinction almost always bears a relation to the importance or the permanence of the barrier separating the supposed new stock from the parent stock." "The contention is not that species are occasionally associated with

¹ See the works of Darwin ('72), Romanes, Weismann ('72), and Nägeli cited in the Bibliography. Weismann's paper relying upon the case of *Planorbis multiformis* in the Steinheim chalk should be considered in connection with Hyatt's Memoir on the same form ('80).

physical barriers, which determine their range, and which have been factors in their formation. It may be claimed that such conditions are virtually universal. In a few cases, a species ranges widely over the earth, showing little change in varying conditions and little susceptibility to the results of isolation. In other cases, there is some possibility that saltations, or suddenly appearing characters, may give rise to a new species within the territory already occupied by the parent form. But these cases are so rare that in ornithology, mammalogy, herpetology, conchology and entomology, they are treated as negligible quantities. In the distribution of fishes the same rules hold good, but as the material for study is relatively far less extensive and less perfectly preserved than with birds and insects, we have correspondingly less certainty as to the actual traits of species and subspecies, and the actual relation of these to the intervening barriers."

President Jordan summarizes the distribution of species in a law, as follows: "Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort." That the intent of the law involves both animal and vegetable kingdoms seems clear from the context.

President Jordan says that his conclusions, much as they differ from *a priori* judgments or the results of experiment, are the unavoidable outcome of the study of distribution, and that they are as a matter of fact "accepted as self-evident by every competent student of species or of the geographical distribution of species."¹

Taking the facts of animal geography as they appear in these several essays, typical of a larger number which might be cited, we may say that as a whole they militate against the operation of Mutation in any wide sense in the animal kingdom. This conclusion is not prompted by the attitude of certain of the zoölogists mentioned, who seem to have made but a cursory study of

¹In a later note in *Science* (N. S., **22**, p. 873) Pres. Jordan modifies his position somewhat, as regards the exclusive agency of spatial isolation and the need of actual physical barriers; but his representation of specific distribution in the animal kingdom is not recast.

the Mutation Theory, but is drawn from the geographic evidence. It is, however, true that the evidence is rather scanty. Moreover there are some exceptions to the general law of distribution, and if these exceptions should, upon further research become very numerous, the prejudicial force of the law would be much diminished. But from the evidence at hand we may infer the very general truth that animal species are distributed according to Jordan's law of geographic isolation; that when exceptions occur, the exceptional species are taken over into some other category of isolation. The nearly universal patch-work character of specific chorology — as at present depicted in the works of zoölogists — strongly suggests the gradual spreading out of individuals over the surface of the earth, their settlement here and there in isolated districts or topographically distinct stations, where shielded from promiscuous intercrossing they have undergone transformations, which have been different in the different areas; transformations which, advancing by whatever forces or conditions, whether those of Natural Selection or of orthogenesis, or what-not, have advanced with even front. This suppositious history is that which forms itself in the imagination of most students of animal geography and has appealed most strongly to me as I have reviewed the literature of the subject.

THE DISTRIBUTION OF PLANTS.

Turning now to the vegetable kingdom we find, first, that there have been few or no exhaustive essays dealing with the question of specific distribution in relation to the theory of evolution. In the second place, it may be said at once that when botanists have turned their attention in this direction their views generally do not coincide with those of the zoologists as to the nature of the facts.

Nägeli ('73) opposed Wagner in a paper of which the purport is succinctly expressed in the title, "*Die gesellschaftliche Entstehung neuer Spezies*," — the social origin of new species. This eminent botanist stoutly opposed Wagner as to the general character of specific distribution, to the study of which he gave much time in the field for several years. He calls particular attention

to the association of species of plants and their varieties upon the same ground, and states that when one form replaces another in consequence of change of ecological conditions within the same district, the replacing form is not related to the other in the closest grade of affinity, but in some degree more remote. He clearly recognizes the intimate relation of distributional studies to the question of evolution.

There is a little bit of evidence from Wallace (:00, p. 391). He says he made inquiries of two experienced English botanists to find whether well-defined varieties occupy areas to the exclusion of the type and do not occupy the area or only a very small one with the type. Only one such case was found in England. Wallace's conclusion is that such varieties of plants occupying considerable areas to the exclusion of the type are not common.

Asa Gray ('59, p. 193) expressed the following opinion: "Whether capable of scientific explanation or not it is certain that related species of phænogamous plants are commonly associated in the same region or are found in comparatively approximate areas, however large, of similar climate."

The case of *Draba verna* L., is most interesting. As is well known, about two hundred distinct species, or at least kinds, of *Draba* have been distinguished within the limits of the original Linnæan species *Draba verna*. These numerous forms were studied in cultivation by A. Jordan, and later by De Bary and F. Rosen. They are found to come true to seed, and for this reason are by these authorities spoken of as species. Their geographic distribution is discussed by both Jordan ('73) and Rosen ('89, p. 613). The conclusion is that as a rule the forms which resemble each other most are found in the same stations. The joint occurrence of next related species is indeed a fact which particularly impressed both of these writers. Rosen thinks that it is very unlikely that these closely related species originated separately and by chance came to be associated in the fashion in which they are now found. Such an explanation might serve, he says, if one or two cases only were to be explained; but it becomes absurd when we consider that the concomitance of next related forms is wide-spread. Rosen ends his account of this group of *Draba* species with a very clear statement of the mutative origin

which he is obliged to assign to these forms; without, of course, using the terms of the Mutation Theory, which he partially anticipates by several years. "The *Erophila* [*Draba*] species owe their existence to the free variation of their forefathers. This consists not in a mere heightening or further development of single characters, but variation fashions new characters and combines old characters in new ways. Therefore the forms which arise from species do not intergrade."

He says that, while Selection plays no part in the origin of these forms it operates upon them after they appear. And of the laws which must control this sort of variation he speaks as follows: "Variation is not blind, vaguely working in all directions, but is obviously determined by laws unknown to us: for we are obliged to assume that the same or similar combinations of next-related forms have arisen in different places. But what can these laws be?" It is most interesting and significant that *Rosen is led to these de Vriesian conclusions through floristic and geographic studies.*

The following excerpt from A. Jordan ('73, p. 4) has so direct a bearing upon our argument that I give it entire: "Ayant observé dans leurs stations diverses, pendant plus de trente années, une foule de végétaux de toutes les familles et de toutes les catégories, des plantes annuelles ou vivaces, bulbeuses ou aquatiques, des arbres ou des arbustes, j'ai pu constater presque partout que lorsqu'un type linnéen, vraiment indigène dans une contrée, y était commun à ce point qu'on pouvait le citer parmi les plantes caractéristiques de la végétation d'une certaine étendue du territoire, ce type y était presque toujours représenté par des formes diverses, plus ou moins nombreuses, *croissant en société et pêle-mêle* [ital. mine]. L'observateur superficiel, qui parcourt le terrain, n'est frappé que des ressemblances de ces diverses formes; il n'aperçoit pas leurs différences, ou, n'y attachant aucune importance, il ne s'arrête pas à les considérer attentivement; il croit n'avoir affaire qu'à un type unique, susceptible de quelques modifications accidentelles et sans valeur. Tandis que celui qui observe avec attention peut aisément se convaincre, sur les lieux, que ces modifications apparentes se retrouvent sur des individus divers, tous parfaitement semblables entre eux. Si,

pour pouvoir continuer et compléter son observation, il arrache des pieds vivants de chacune des formes qu'il a pu distinguer et les replante ensuite, dans un même lieu, afin de les suivre dans tous leurs développements, il se convaincra bientôt qu'elles présentent des différences appréciables, dans tous leurs organes. S'il sème leurs graines, il les verra se reproduire avec une parfaite identité de caractères.

“Voilà le fait que j'ai pu constater moi-même mille fois, que j'ai fait constater dans les lieux que je ne pouvais visiter, en France, en Corse et en Algérie ou ailleurs, par divers botanists qui m'ont envoyé soit des graines, soit des pieds vivants de formes nombreuses, recueillis dans les mêmes station et appartenant aux memes types linnéens. Je ne dis pas que les plants communes soient toutes également et partout diversifiées. Il y a, sous ce rapport, de grandes différences entre elles. Je dis seulement que *le cas où elles présentent diverses formes croissant en société est le cas le plus ordinaire* [ital. mine], et je crois que ce fait paraîtra clair, patent, indiscutable, à quiconque prendra la peine de le vérifier sérieusement.”

In the literature of this subject, as far as I have read it, essentially the only writers who insist on the isolation of nearly related kinds of plants are the zoologists. Their assertions are not, however, supported by evidence from the vegetable realm.

I have examined the distribution of North American Orchidaceæ from the standpoint of this paper. Furthermore, I have consulted with several specialists in different groups as occasion offered. Several members of this club have given me information with permission to publish it along with the evidence gathered by myself. I may take the groups in sequence.

For Algæ, Mr. F. S. Collins speaks as follows in regard to their general distribution and in particular the distribution of nearest related species: “As regards fresh water algæ, it almost seems as if geographical limitations did not exist. Of course this is not entirely true, but the area of distribution in the case of the great majority of fresh water algæ is vastly greater than in the

case of most flowering plants.¹ The limitations seem to be those of temperature, exposure, character of attachment, and to a less degree, geological characters. Take the genus *Vaucheria*, for instance. The last serious work is by Götz; a study of the species of *Vaucheria* in the neighborhood of Basel, Switzerland. There are 12 species there; 8 of them occur in England, 6 in the New England States, 7 in California. Only three other fresh water species are recorded for North America; one is a European species, found in the West Indies but not elsewhere so far on this continent; the other two are from California. Now these two species, growing together, belong to the same subgenus, and I know of no described species that I should say belonged in between them. Take the genus *Spirogyra*. The best book on this is that of Petit, *Spirogyres des Environs de Paris*. He includes 37 species; of these 34 have been found in North America. We have also five other species; three of them are European, though not found about Paris; the two others are from Greenland and Florida respectively. It is much the same with all the fresh water algæ; of the very inconspicuous species, the records from distant stations are not so abundant, but that is largely because these minute forms have been little studied outside of Europe.

"As to the marine algæ, the difference geographically is much greater. It would seem strange that marine algæ on the two sides of the Atlantic, should differ much more than the fresh water algæ of the two continents, but such is the fact. Still the resemblances are much greater than with flowering plants. And there are many instances where closely allied species or varieties have practically the same range. I will give a few such pairs, and in each case there seems to be no species or variety anywhere else that would stand between the two in question.

"*Cladostephus verticillatus* and *C. spongiosus* have the same range, in temperate waters on both sides of the Atlantic. They are the only species of the genus in that range. *Fucus edentatus* and *F. evanescens* have their headquarters in high arctic regions,

¹ Compare Alph. De Candolle, *Geographie Botanique*, 1, p. 499: "Nous arrivons ainsi à une loi importante, savoir que l'aire moyenne des espèces est d'autant plus petite que la classe dont elles font partie a une organisation plus complète, plus développée, ou, selon l'expression usitée, plus parfaite."

extending to Great Britain, New Jersey and California. *Myrio-trichia filiformis* and *M. clavæformis* have practically the same range as the *Cladostephus* species. *Ralfsia borneti* and *R. verrucosa* have a slightly more northern range on both sides of the Atlantic. *Phyllophora brodiaei* and *P. membranifolia* range from France and New Jersey to Norway and Labrador. *Polysiphonia violacea* and *P. fibrillosa* from Virginia to Maine, from the Mediterranean to Scotland. *P. harveyi* and *P. olneyi* are American species, or possibly varieties of the same species; they have the same range as *P. violacea* and *P. fibrillosa*; wherever I found one, I should expect to find the other.

"I could keep on for some time in this way, but will give only one more instance; that is a group of species in the genus *Antithamnion*, one of the most beautiful of the red algæ. On the European coast *A. plumula* ranges from Morocco to Great Britain; *A. cruciata* about the same; *A. floccosa* from the English channel to high arctic regions; *A. boreale* from the Faroes north; *A. pylaisæi* from Norway north. On the American coast *A. plumula* and *A. cruciatum* range from New Jersey to Cape Cod; *A. floccosum* and *A. boreale* from Cape Cod to Greenland; *A. pylaisæi* from Long Island Sound to Greenland; *A. americanum* from New Jersey to Portland, Maine. On our Pacific coast *A. floccosum* ranges from California to Alaska; *A. boreale* from southern Alaska to high arctic regions; *A. pylaisæi* from Washington north. Now these are all so closely allied that Rosenvinge some time ago proposed to unite them all under the older name, *A. plumula*. He is a man with a strong tendency toward uniting, it is true, and has since concluded that *A. cruciatum*, and possibly *A. floccosum* are distinct; but at any rate, this shows how closely allied they are.

"Some things about algæ seem very much like supporting the mutation theory; when the same species occurs in widely distant stations, we sometimes find with the type exactly the same varieties and forms."

Dr. Evans, while lacking the opportunity to pay very extended attention to the subject, has given me the following indication of the distributional conditions in Hepaticæ. "One of the best examples of a cognate pair of species is *Leptolejeunea elliptica*

and *L. exocellata*. The first of these species is very widely distributed in tropical America, growing on the upper surface of thick and glossy leaves. The second species is less abundant but nearly always occurs mixed with the first.

"Among northern species *Lophozia barbata* and *L. lyoni* are closely related and often grow together, although each retains its distinctive characteristics. The same is true of *Gymnomitrium concinnatum* and the much rarer *G. corolloides*; of *Sphenobolus exsectus* and *S. exsectiformis*; of *Anthoceros levis* and *A. punctatus*.

"As a group of related species I might mention the ventricosa-group of the genus *Lophozia*. This contains about half a dozen closely related species, most of which are circumpolar in their distribution. *L. ventricosa*, *L. alpestris*, *L. porphyroleuca*, *L. longidens* and *L. confertifolia* are all known from New England, being most abundant in mountainous regions. Of these *L. porphyroleuca* and *L. longidens* grow on rotten logs, and the others on moist rocks, although *L. longidens* is equally at home on either substratum. Although I have no definite data that these species actually grow mixed in North America, their ranges coincide to a greater or less extent with some overlapping.

"Unfortunately our information is not very full at present about the distribution of many species. Only a few regions have been at all accurately studied, and I feel sure that further study would considerably lengthen the short list I have given."

Mr. A. A. Eaton has given me several examples from *Equisetum* and *Isoetes*. "*Equisetum fluviatile* is circumboreal in its distribution. No third form stands between this and *E. palustre*, yet the latter has practically the same range. *E. scirpoides* and *E. variegatum* are a cognate pair, and yet both have in general the same range throughout the northern part of both hemispheres. *E. variegatum* has a variety, *E. variegatum jessupi*, distinguished by anatomical characters. Its range, Vermont to Minnesota, is quite covered by that of the species. *E. laevigatum* has a near relation, without an intermediate, in *E. hiemale intermedium*, and this on the other side is next to the variety *affine*. The last of the trio is wide-spread in northern North America and overlies the other varieties, which also essentially coincide in their ranges. *E. arvense* is found in Europe, Asia, N. America to Virginia and

southern California. Its near of kin (without intermediate), *E. telmateia*, is found with it (broadly speaking) in Europe and California. Starting with *E. pratense* a next-related species is *E. sylvaticum*. The former belongs to northern Europe, Siberia, Alaska, Canada, the Rocky Mountains, Labrador, and southward to Massachusetts and New Jersey. The other is circum-boreal, covers the range of the first and with us goes somewhat further south to Virginia.

"In *Isoetes* we find the following coincident ranges of close relatives. *Isoetes tuckermanni* is found quite plentifully in New England and completely overlies the range of its varieties *harveyi* and *borealis*. *I. engelmanni* is found plentifully throughout the region east of the Appalachian range, from New Hampshire and Vermont to Pennsylvania, extending sparingly to Georgia. It overlies the ranges of its varieties *caroliniana*, *fontana* and *valida*. *I. canadensis* is found from Pennsylvania to Maine and Quebec, appearing again in British Columbia. Its next of kin in the genus is *I. engelmanni*, whose range for the most part it covers, and the two species are not rarely found commingled in the same pond. *I. bolanderi* is found from Wyoming to California and Washington. Its next of kin would appear to be *I. pygmaea* of the Mono Lake region of California, and the two species were found by members of the King Expedition in contiguous areas. It may be supposed that *I. pygmaea* is an abnormal form of *I. bolanderi* and hence not competent in this relation, but the next of kin of *bolanderi* is *I. echinospora* var. *braunii*, which overlies the range of *bolanderi*, but is widely distributed otherwise in North America."

I have inquired of President Brainerd about the conditions in *Viola*, and particularly whether pairs of closely related species are found within the same ranges. He answers: "Many pairs of species in *Viola* closely allied and nearly co-extensive in range are to be found." He mentions six of them; viz. (1) *V. fimbriatula* and *sagitata*, (2) *V. palmata* and *papilionacea*, (3) *V. septemloba* and *emarginata*, (4) *V. lanceolata* and *primulaefolia*, (5) *V. ranifolia* and *incognita*, (6) *V. arenaria* and *conspersa*. These are without intermediate species says President Brainerd, but they have intermediates resulting from hybridization, found in the same localities with the species.

To Professor Charles Sprague Sargent I am indebted for interesting information as to the distribution of North American *Cratægus*. As is well known, numerous species have been distinguished within the last few years, of which some five hundred have been named. These species are readily and unmistakably recognized by special students of the genus, by means of floral characters such as number of stamens, color of anthers, form of inflorescence, etc.; by fruit characters, configuration of nutlet, time of blooming and fruiting, character of foliage, veining, presence or absence of hairs, etc.; traits which appear to be constant and reliable as shown by extended observation in the field and by cultures of seedlings carried on now for a number of years at the Arnold Arboretum. In these cultures, the sowings from the several species result in crops of seedlings of remarkable uniformity within the limits of each species, and in the instances in which the seedlings have flowered and fruited, of notable conformity to parental type. This result must certainly diminish the scepticism with which the proposal of such a vast number of species within the one genus has rather naturally been met in some quarters.

In answer to the question whether the nearest related species are separated, as the law of D. S. Jordan and of Wagner would require, Professor Sargent replies in the negative.

In the genus as it is represented in North America several groups are distinguished, which in part correspond to the species of the older writers, and which may be readily recognized by anyone with a little attention. such are *Crus-galli*, *Punctatæ*, *Æstivales*, *Tenuifoliæ*, *Pruinosæ*, *Intricatæ*, *Flabellatæ*, *Anomalæ*, *Molles*, *Tomentosæ*, etc. These groups are in general fairly well restricted to particular geographic sections. For example, the *Tenuifoliæ*, the largest group in the northeast, do not extend west of the Mississippi river, or go southward except along the mountains. The *Flavæ* are found only in the southeast. The *Intricatæ* are most numerous in eastern Pennsylvania, extending along the mountains southward to the end of the Alleghanies, northward into Vermont, and westward through New York and Ontario to southern Michigan, within which distributional area they mingle with all the other northern groups. In some cases a group

predominates in a region, in other regions several groups are nearly equally represented. Within each group, divisions can be made; but in the case of these divisions geographic separation does not obtain, since species of all the divisions of a group are likely to occur in any part of the general territory proper to the whole group. Regarding the ultimate units, or species, those which are most closely allied are likely to be found promiscuously associated in the same district and without the semblance of isolation. For example species of the *Pruinosæ* or of the *Intricatæ* with 10, or with 20 stamens, or with rose-colored, or with yellow anthers are found growing within a few feet of one another, and may cover common districts of several hundred square miles. In these cases, while it is the number of stamens or color of anther which first attracts attention, other specific characters exist which adequately distinguish the species. As an example of promiscuous association, the vicinity of Albany may be pointed out, where the five species of *Intricatæ* heretofore found in New York state grow in a small area. In Ontario we find twenty-five species of *Tomentosæ*, many of them growing very close together. In the distinctly southern group *Microcarpæ* we find the two species, *C. apiifolia* and *C. spathulata*, growing over the same areas, while the third and more distantly related species, *C. cordata* has a somewhat more northern range. In general, the reverse of Jordan's law would more nearly represent the distribution of American species of *Cratægus*.

Coming now to *Orchidaceæ*, I may say that I adopted the line of examination suggested by the form of Jordan's law; that is, I looked for pairs of kinds. I say kinds instead of species intentionally. The main problem should not be confused by the difficulty of agreeing upon a definition of species. What the evolutionist has to account for is not the definitions of systematists, but the multiplicity of hereditary types; he has to explain the antithesis between the uniformity which heredity seems at first to promise, and the diversity which actually prevails among organic things. A definition of species is demanded in taxonomy, but is somewhat less necessary in studies like the present. We do not require that the forms be related in some particular taxonomic sense; but only that they have different hereditary charac-

ters. In order to avoid complications I have used the word *kind* to designate such different types, instead of the words species, variety, etc., which have restricted technical senses.

I have sought for closely related pairs of kinds so made up that in each case no third kind stands between the members of the pair in resemblance. Such pairs I may call immediately cognate pairs, or for short, cognate pairs. A pair may consist of two species, two varieties, two subspecies, a species and a subspecies, a species and a variety, etc. It is assumed that such cognate pairs represent recent forkings of the phylogenetic tree; and that if we could collect all such cognate pairs in the vegetable kingdom we should have a representation of all the youngest forkings. Evidently their distribution would be very illuminating, for the youngest branches are on the average the least disturbed geographically, and the distribution of the members of these pairs would represent as accurately as we could ever discover it, the position of things at the moment when forking takes place. That is, we should have a geographic chart, more or less distorted it is true, of the origin of kinds. If the members of the pairs are universally, in the vegetable kingdom, separated from each other, then — as already explained — Mutation is excluded as a true cause of diversification of hereditary types in plants. For among several forms of isolation to which Mutation may conceivably give rise, and which are, therefore, not inconsistent with the mutational assumption, the one form of isolation to which it could never give rise is geographic isolation.

I repeat that I have examined only the broad geographical aspect of distribution and not at all the topographical, for which exact data are wanting. Let the reader recall the two stages of this general inquiry: my evidence belongs to the first of these. I present the following facts as a contribution towards an answer to the question, Is Mutation instantly excluded from a place among the considerable powers in evolution, by the broad aspects of specific distribution in plants? I have taken only one step. But this may be of some little importance, especially in view of the assertions concerning the distribution of plants which have been made, and in view of the lack of even broadly geographical statistics.

EVIDENCE FROM THE FAMILY ORCHIDACEÆ IN NORTH AMERICA

The American *Habenarias* have been given careful study in our laboratory. In addition to our own collections, those from several of the largest herbaria in the United States have been brought together. The species have been delimited with minute attention and then the distribution of each species, represented by the large amount of material assembled, has been recorded. Thus exceptionally full and reliable returns have been secured, which are available for the present paper.

H. ciliaris R. Br., and *H. blephariglottis* Torr., are a pair of perfectly distinct, yet extremely similar species. While instantly distinguishable in the field by their colors — the flowers of the former being yellow or orange, those of *H. blephariglottis* pure white — the dried specimens are separated only upon close inspection. The best distinguishing character is then the degree of fimbriation of the lip, which is considerably greater in *H. ciliaris* than in *H. blephariglottis*. No third species stands between them. They are spread together through the eastern United States. *H. ciliaris* is found in Massachusetts, Connecticut, New York, Ontario, Michigan, New Jersey, Pennsylvania, Ohio, Indiana, Delaware, Maryland, District of Columbia, Virginia, Kentucky, North Carolina, Tennessee, Missouri, Arkansas, S. Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Texas. *H. blephariglottis* is found in Newfoundland, Nova Scotia, New Brunswick, all New England, New York, Ontario, Michigan, New Jersey, Pennsylvania, Ohio, Virginia and North Carolina; and if we include the southern form which may possibly be distinguished, the range is extended to South Carolina, Georgia, Alabama, and Mississippi. Whether we allow that the southern form is distinct or not is immaterial, since it does not stand between *H. blephariglottis* and *H. ciliaris*, and the latter species covers the range of both the northern and the southern forms of the other.

H. cristata R. Br., *H. chapmanii* Ames, and *H. ciliaris* R. Br., form a group of very closely related kinds. *H. cristata* is like a very small *H. ciliaris*, with a broader and un-clawed lip, petals oblong or somewhat obovate instead of linear, and a spur

shorter than the ovary instead of longer. *H. chapmanii* is intermediate between the others in perhaps every respect, and this fact, with the absence of any new character of its own, makes this species appear very like a hybrid. Its apparently local occurrence is in favor of hybridity. But allowing it to be independent, it forms a pair with *H. cristata* on one side, and with *H. ciliaris* on the other. On the other hand, removing the plants now grouped as *H. chapmanii*, because of suspected hybrid origin, we have left a very close pair in the two supposed parental types. On any disposition of the matter, the geographical ranges of the three kinds are found to coincide widely. The range of *H. ciliaris*, as above shown, extends from New England to middle Florida and Texas, and inland to Michigan, Missouri and Arkansas. That of *H. cristata* includes all the Atlantic states from New Jersey to Louisiana, with Pennsylvania, Tennessee and Arkansas added. Specimens of *H. chapmanii* have been seen only from northern Florida.

Habenaria psycodes Gray, and *H. fimbriata* R. Br. are a very close pair, with no intermediary. They are with some difficulty distinguished, yet statistical studies that I made upon them some time since convinced me that authors, including the most reliable authorities, are right in considering them specifically distinct. No one character can be relied upon to separate them invariably but all characters of each species fluctuate, so that any given part in one may run into the form characteristic of the other species. The balance of characters, however, is almost always decisive. The geographic ranges are very largely the same. Both are found in Newfoundland, Nova Scotia, New Brunswick, Quebec, all New England, New York, New Jersey, Pennsylvania, and North Carolina. *H. psycodes* extends further west, and *H. fimbriata* a little further south, as represented in the collections before me.

H. peramæna Gray, has for its probably nearest relative *H. fimbriata* — or possibly *H. psycodes* — with no species between. The three species mentioned, with *H. leucophæa*, form a group of close affinity. While *H. peramæna* is more widely distributed westward and southward (Ill., Mo., Ala.), and *H. fimbriata* much further northward, they occupy extensive territory together; viz.,

Pennsylvania, West Virginia, North Carolina, and Tennessee. If *H. psycodes* is substituted for *H. fimbriata* in the comparison, the geographic result has the same influence on the discussion.

H. orbiculata Torr. and *H. macrophylla* Goldie are so close that the plants of the two kinds have long been accepted by collectors and described by authors as of one species. The differences are at first sight slight, but are apparently constant and sufficient for distinction. The former species has a much greater range, which completely covers that of the latter. *H. orbiculata* extends from Labrador and Newfoundland westward through Michigan, and Minnesota, to British Columbia and Washington; and southward through New England, New York, and Pennsylvania to South Carolina and Tennessee. It is found in every district where *H. macrophylla* is found; viz., Newfoundland, New Brunswick, Ontario, Michigan, New England, and New York. The status of these two species is discussed by Ames in *Rhodora* for January, 1906, with illustrations of the flowers.

The difficult genus *Spiranthes* has lately been thoroughly studied by Ames, who has given the results in *Orchidaceæ*, Fasc. I, pp. 113-154. The abundance of material examined may be seen from the citations of specimens in the detailed statement of the distribution of each species.

S. cernua Rich. has for nearest allies, first, the variety (which some authors regard as a species), *S. cernua* var. *ochroleuca* Ames, and secondly the species *S. odorata* Lindl. *S. cernua* may be paired with either of them. *S. cernua* and *S. cernua ochroleuca* in the dried state can be separated with certainty by no macroscopic character. They may be distinguished by the seeds, however, *S. cernua* being polyembryonic.¹ Unfruited specimens being indistinguishable in the dry state, the exact distribution of each form may not be very precisely defined, but Rydberg in Britton's *Manual* gives the range of var. *ochroleuca* as from New Hampshire and Massachusetts to Pennsylvania and North Carolina. I myself have identified, as being unmistakably typical *S. cernua*, specimens from Massachusetts, Ontario, Iowa, and Georgia.

¹ See my notes on the embryology of the two forms in *Rhodora* **2**, p. 227 (1900) and **3**, p. 61 (1901). In *S. cernua* embryo formation takes place without pollination.

Thus the range of the species overlies that of the variety. Geographic isolation is wanting.

When we compare *S. cernua* with *S. odorata* we find again a very strong likeness. *S. odorata* is usually much larger in all parts than the former. The length of the scape relative to that of the leaves is greater in *S. odorata*, and its leaves are less strictly radical. Those not expert in the genus *Spiranthes* would often distinguish the two species with difficulty. They might be regarded as elementary species in de Vries's sense. *S. odorata* has been found in Virginia, Georgia, Florida, Alabama, Louisiana, and Texas, and its range thus coincides widely with that of *S. cernua*.

S. romanzoffiana Cham. and *S. porrifolia* Lindl. are very closely related species, which no other species approaches. The former is by very much the more widely dispersed, since it crosses the continent, while *S. porrifolia* is confined — according to specimens seen — within the states of Washington, Oregon, and California. *S. romanzoffiana* is represented in our records by many specimens from these same states, and there is therefore no general geographic separation in this case.

S. laciniata Ames and *S. vernalis* Engelm. and Gray are extremely similar but distinct species. The former is confined to Georgia, Florida, Alabama, Louisiana and Texas. *S. vernalis* occurs in all these states, but reaches far beyond this area.

S. beckii Lindl. and *S. gracilis* Beck are an immediately cognate pair of near affinity. The former grows in the Atlantic states from Massachusetts to Texas. *S. gracilis* covers the same range, but is also to be found further north and further inland. There is no geographic isolation.

Cypripedium pubescens Willd. and *C. parviflorum* Salisb. have had attention at this laboratory for several years, observations having been made in the field and in the herbarium, and collections of dried specimens having been received from many sources. Measurements indicate that there are two pronounced tendencies as regards size of flower. In life, the plants generally have an appearance of distinctness, and most field naturalists whose opinions have been asked, have maintained that the two kinds are specifically different. The manuals treat them so. Yet they

occasionally intergrade and perhaps can be regarded merely as subspecies. I have found them growing together in closest proximity. We have specimens of *C. parviflorum* from Ontario, British Columbia, New England, New York, New Jersey, Pennsylvania, Ohio, Indiana, Michigan, Wisconsin, Washington; and of *C. pubescens* from New England, New York, Pennsylvania, Ohio, Illinois, Wisconsin and Minnesota. The manuals extend the reported occurrence of both plants to Georgia. Thus the ranges of these two very closely allied kinds coincide over a very wide extent of territory. No other form in the world stands between them.

The genus *Calopogon* is confined to the eastern half of the United States (if we except the occurrence of *C. pulchellus* in Cuba), and comprises four close species and a variety, or five species. These species all come together and overlap in Florida. One, *C. pulchellus* R. Br., ranges from Newfoundland to Florida, Cuba, and Missouri, and geographically includes all the rest. *C. pallidus* Chapm. ranges from North Carolina to Florida and Alabama; *C. parviflorus* Lindl. from North Carolina to Florida; *C. multiflorus* Lindl. is confined to Florida. Here, therefore, are several pairs of cognate species not geographically separated.

Pogonia verticillata Nutt. and *P. affinis* Austin make a pair of very nearly related yet distinct species. The former extends from New England to Florida and west to Wisconsin and quite surrounds the other, a very rare species occurring sporadically in Vermont, Massachusetts, Connecticut, New York and New Jersey. Here again geographic isolation is wanting.

The conclusion from this examination of North American Orchidaceæ is that cognate pairs of kinds with uniform or widely coincident ranges are too numerous to leave any force at all in Jordan's law in its broad sense as regards this family in our flora. If one member of each pair was derived from the other member, or both were derived from a parent species, then, *as far as the geographic evidence goes, the new species may have originated in the same district with the old one; i. e. without geographic isolation.*

CONCLUDING REMARKS.

In concluding this paper I may make some remarks of a general character touching the whole problem.

First, we note that zoologists and botanists are rather distinctly opposed to each other in their views of the actual state of specific distribution. The suggestion is offered that zoologists may best discover the condition and interpret its meaning among animals, and botanists among plants. In no case is it safe to reason deductively from one kingdom to the other. In the factors affecting their evolution plants and animals differ vastly.

Secondly, in seeking for the laws of specific distribution we should first take the facts as we find them. We should agree to consider that in the absence of explicit evidence to the contrary, kinds now found in coincident ranges have been so situated from the beginning. In any given cases this assumption may or may not represent the truth, but we have no right to postulate movements in the past, of which there is no certain evidence, in order to save a preconceived theory. We may call such hypothetical migrations into being, in a strictly limited number of cases, upon a reconsideration, if from a first examination of the unmodified facts some law emerges so strong and compulsory that the few exceptional instances must somehow be brought into accord with it.

In the third place, if I may express my personal impression of the matter with regard to plants, it seems to me that the study of specific distribution in the vegetable kingdom is not likely to be unfavorable to Mutation, regarded as a method, but perhaps not the sole method, of evolution. It is true that in examining the distribution of species of plants, one encounters an effect which seems to be connected with geographical distance. We often find that a species of wide distribution exhibits slightly different phases in different divisions of its range. These phases are sometimes too subtle for definition and pass into one another by degrees, yet are evident to students of particular groups. Such cases do not look like the work of Mutation. They exemplify that which, to conceal ignorance of causes, may be termed a geographic effect.

But this aside, the indications seem to me to be that a good many instances sustaining the notion of mutative origin will be found among plants. It is not to be expected that the number of such cases will be *relatively* large. On the assumption of periodic Mutation as the origin of species, with competition between associated mutants and the survival of those mutants best fitted for existence in the original habitat, and the spread of mutants with new capacities into areas or habitats not open to the parental species, we should expect to find as a rule a single species occupying a given territory or ecological footing, and related species in separate, neighboring areas or habitats; though it is evident that mutants instantly endowed by Mutation with physiological or choral isolation might continue to exist side by side with the parental species or with sister mutants if there were no active vegetative competition between the associated stocks. As a matter of fact, in many species of plants competition for subsistence between individuals of the same parentage is practically absent. Unification of congenital mutants may be brought about by continued interbreeding. This would eventually destroy the geographic evidence of Mutation in any given case. But in such amalgamation the effects of Mutation may not be destroyed; for new characters may during amalgamation be perpetuated in full force. It is single characters, rather than constellations of characters, with which the Mutation Theory is primarily concerned. The number of cases of association of closely related species resembling recent mutants, in proportion to the number of cases of geographic or topographic segregation of closely related species would depend upon the balance between the activity of Mutation on the one hand and the operation of the forces tending to isolate or to amalgamate the products of Mutation on the other. If mutative periods are far apart in most species — and stability of the organic world may preclude great frequency — while the segregating or amalgamating powers are constantly at work, then the occurrence of the social condition indicative of Mutation may be expected to be relatively infrequent.

In order to use geographical evidence effectively against the Mutation Theory, its opponents must show that the social condition of closely related forms is, to use President Jordan's words,

“virtually unknown.” In the vegetable kingdom this is likely to be an arduous task. The indications are that the adherents of Mutation will be able to bring forward enough cases of social distribution to render phytogeographic weapons useless in the attack upon this Theory.

THE AMES BOTANICAL LABORATORY,
NORTH EASTON, MASS.

LITERATURE

CASTLE, W. E., AND FORBES, ALEXANDER.

1906. Heredity of Hair-length in Guinea-pigs and its bearing on the theory of pure gametes. Published by the Carnegie Institution of Washington, D. C.

DARWIN, CHARLES.

1859. The Origin of Species, chapters 11 and 12, on Geographical Distribution.

1872. The Origin of Species, 6th Edition, chapter 4, as far as it relates to Isolation and to Divergence of Character.

DAVENPORT, C. B.

1906. Inheritance in Poultry. Published by the Carnegie Institution of Washington, D. C.

DE VRIES, H.

1903. Die Mutationstheorie, **2**, pp. 396–457 (die Mutationskreuzungen).

GULICK, REV. J. T.

1887. Divergent evolution through cumulative segregation. Jour. Linn. Soc., Zool., **20**, p. 189.

1905. Evolution, racial and habitudinal. Published by the Carnegie Institution of Washington, D. C.

HYATT, ALPHEUS.

1880. The genesis of the tertiary species of Planorbis at Steinheim. Anniversary Mem. Boston Soc. Nat. Hist. 1880.

JORDAN, ALEXIS.

1873. Remarques sur le fait de l'existence en société, à l'état sauvage des espèces végétales affines et sur d'autres faits relatifs à la question de l'espèce. Lyon, Pitrat Ainé (pp. 23).

JORDAN, PRESIDENT DAVID STARR.

1905. The Origin of species through isolation. Science, N. S., **22**, p. 545. In the same volume, p. 873, appears a note modifying some statements of the above paper.

MACDOUGAL, D. T.

- 1906.** Discontinuous variations in pedigree cultures. Pop. Sci. Monthly, Sept., 1906.

MERRIAM, C. HART.

- 1906.** Is Mutation a factor in the evolution of the higher vertebrates? Proc. A. A. A. S., New Orleans, 1906, p. 383. Also Science, N. S., **23**, p. 241 (1906).

NÄGELI, C.

- 1873.** Die gesellschaftliche Entstehung neuer Spezies. Sitzungsbd. math.-phys. Klasse d. k. b. Akad. München, **3**, p. 305 (1872-3).

ROMANES, G. J.

- 1886.** Physiological Selection. Jour. Linn. Soc., Zool., **19**, p. 337.

- 1906.** Darwin and after Darwin. Vol. 3, Isolation and physiological selection. Opinions on isolation [with clues to valuable data of distribution]. The appendices contain important matter.

ROSEN, F.

- 1889.** Systematische und biologische Beobachtungen über *Erophila* [Draba] verna. Bot. Zeit., **47**, pp. 565, 581, 597, 613.

WAGNER, MORITZ.

- 1889.** Die Entstehung der Arten durch räumliche Sonderung. Gesammelte Aufsätze. Basel. This edition contains the following papers of importance: Die Darwin'sche Theorie und das Migrationsgesetz der Organismen. Leipzig, 1868.— Ueber den Einfluss der geographischen Isolirung und Kolonienbildung auf die morphologischen Veränderung der Organismen. München, 1870, Sitzungsbd. d. k. bayer. Akad. Wiss. 2 July (1870).— Ueber die Entstehung der Arten durch Absonderung. Kosmos, Hfte. 1, 2, 3, (1880).— Darwinistische Streitfragen [5 papers]. Kosmos (1882, 1884).

WALLACE, ALFRED RUSSELL.

- 1855.** On the law which has regulated the introduction of new species. Annals and Magazine of Nat. History, September, 1855. Also in his Contributions to Natural Selection, London, 1875, p. 5.

- 1900.** Studies, scientific and social, **2**, p. 391.

WEISMANN, AUGUST.

- 1872.** Ueber den Einfluss der Isolirung auf die Artbildung. Leipzig, Engelmann.

- 1904.** The Evolution Theory. Tr. by Thomson. London, E. Arnold. Vol. 2, ch. 32, Influence of isolation on the formation of species. Also **2**, p. 350.